Neuropsychologia 117 (2018) 199–210

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Disentangling representations of shape and action components in the tool network

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ARTICLE INFO

Keywords:
Object representation
Tool network
Shape
Action
Pattern analysis
fMRI

ABSTRACT

Shape and how they should be used are two key components of our knowledge about tools. Viewing tools preferentially activated a frontoparietal and occipitotemporal network, with dorsal regions implicated in computation of tool-related actions and ventral areas in shape representation. As shape and manners of manipulation are highly correlated for daily tools, whether they are independently represented in different regions remains inconclusive. In the current study, we collected fMRI data when participants viewed blocks of pictures of four daily tools (i.e., paintbrush, corkscrew, screwdriver, razor) where shape and action (manner of manipulation for functional use) were orthogonally manipulated, to tease apart these two dimensions. Behavioral similarity judgments tapping on object shape and finer aspects of actions (i.e., manners of motion, magnitude of arm movement, configuration of hand) were also collected to further disentangle the representation of object shape and different action components. Information analysis and representational similarity analysis were conducted on regional neural activation patterns of the tool-preferring network. In both analyses, the bilateral lateral occipitotemporal cortex showed robust shape representations but could not effectively distinguish between tool-use actions. The frontal and precentral regions represented kinematic action components, whereas the left parietal region (in information analyses) exhibited coding of both shape and tool-use action. By teasing apart shape and action components, we found both dissociation and association of them within the tool network. Taken together, our study disentangles representations for object shape from finer tool-use action components in the tool network, revealing the potential dissociable roles different tool-preferring regions play in tool processing.

1. Introduction

Viewing different domains of objects relatively selectively recruit different brain networks (Kanwisher et al., 1997; Epstein and Kanwisher, 1998; Chao et al., 1999; Haxby et al., 2000; Epstein, 2005, 2008; Peelen and Downing, 2005; Schwarzlose et al., 2005; Lewis, 2006; Tsao et al., 2008; He et al., 2013; Grill-Spector and Weiner, 2014; Hutchison et al., 2014). Among them, compare to pictures of categories of objects, viewing tool pictures activate more strongly a cortical network including left-lateralized inferior frontal cortex, precentral and premotor cortex, inferior and superior parietal cortex, lateral occipitotemporal cortex (LOTC) and bilateral medial fusiform gyrus (Martin et al., 1996; Chao et al., 1999; Chao and Martin, 2000; Noppeney et al., 2006; Mahon et al., 2007; see Lewis, 2006; Mahon and Caramazza, 2009; Martin, 2007 for reviews). What are the representation contents in these regions make them more sensitive to tools?

The most widely assumed properties that drive the tool-selectivity, and thus are assumed to be represented in these regions, are manipulation-action-related properties. Tools are tightly associated with specific manipulation-actions in human daily life, and more so than other object categories such as animals (Mruczek et al., 2013; Chen et al., 2017a). The main kind of interactions we have with tools are manipulating them in certain manners (usually grasping with hand and manipulating with both hand and arm) to achieve specific functions. Findings from previous studies indicated that manipulation knowledge was a critical component of tool concepts (Warrington and McCarthy, 1987; Buxbaum et al., 2000; Buxbaum and Saffran, 2002; Kellenbach et al., 2003; Bub and Masson, 2006; Watson et al., 2014; but see Vannuscorps et al., 2014; Zinchenko and Snedeker, 2011) Neuropsychological and neuroimaging studies found that the frontoparietal

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https://doi.org/10.1016/j.neuropsychologia.2018.05.026
Received 8 September 2017; Received in revised form 6 May 2018; Accepted 29 May 2018
Available online 30 May 2018
0028-3932/

cortex and LOTC within which tool-selective activations were frequently observed and their underlying white-matter pathways, were also frequently shown to be involved in action recognition and production as well as action (manipulation) knowledge retrieval (Buxbaum et al., 2000, 2007; Buxbaum and Saffran, 2002; Tranel et al., 2003; Lewis, 2006; Negri et al., 2007; Kalénine et al., 2010; Bi et al., 2015; Tarhan et al., 2015; Lingnau and Downing, 2015; Chen et al., 2016, 2017b; Buxbaum, 2017). Even the occipitotemporal regions which were classically assumed to represent object shapes (James et al., 2003; Haushofer et al., 2008; Karnath et al., 2009; Peelen and Caramazza, 2012; Peelen et al., 2014) could differentiate between tools with different manners of manipulation (Chen et al., 2016, in and around extrastriate body area), make predictions of upcoming motor actions through activation patterns (Gallivan et al., 2013), and exhibit motor-related repetition suppression effect (Mahon et al., 2007).

Another potential dimension is the object shape. Previous neuropsychological studies found that lesions to occipitotemporal regions led to visual object agnosia with relatively retained object-directed movements (Goodale et al., 1991; James et al., 2003; Karnath et al., 2009). The neural activation patterns in ventral occipitotemporal regions have been reported to code object shape information (Haushofer et al., 2008; Peelen and Caramazza, 2012; Peelen et al., 2014; Bracci and Op de Beeck, 2016; Proklova et al., 2016; Chen et al., 2017a). In addition to the ventral stream regions that have long been implicated in object form processing, recent empirical findings suggested that cortical regions in the parietal cortex also process information about object shapes or identities (Konen and Kastner, 2008; Zachariou et al., 2014; Jeong and Xu, 2016; Chen et al., 2017a; see Freud et al., 2016 for a review). Thus, it is possible that regions in the tool network process object shape representations and the tool selectivity there might reflect their functional preference to particular types of shapes. A recent study has investigated whether elongated shape plays a critical role in tool-selective activation (Chen et al., 2017a). They found that elongation could account for the tool selectivity in dorsal occipital and the premotor regions but did not affect the activation strength in the anterior inferior parietal region, and coding of elongation and toolness (i.e., tools vs. non-tools) coexists in the left MTG. These results highlighted the possible role of object shape in driving tool selectivity. However, what properties underlie the “toolness” and whether the elongation of object correlated with certain action properties was not investigated in this study.

Critically, object shapes and object-directed actions tend to be correlated, given that different shape offers different affordance for specific actions such as grasping and/or manners of manipulation (Riddoch et al., 1988; Caramazza et al., 1990; Mahon and Caramazza, 2009; Bi et al., 2016). These two properties were rarely investigated together and their effects could not be disentangled. We are aware of only two studies about tools that included both shape and action conditions, although their primary interests were not about which of these variables explained tool selectivity (Peelen and Caramazza, 2012; Bracci et al., 2017). Both studies looked at specific effects of shape and action properties with the other variable controlled for and obtained different results. Peelen and Caramazza (2012) showed action-specific information (rotate vs. squeeze) only in the anterior temporal lobe and shape-specific information in only the posterior LOTC. Bracci et al. (2017), by contrast, reported action-only (i.e., hand action/manipulation) effects in prefrontal areas, and both action- and shape-effects in parietal and occipitotemporal areas, although the latter two regions had different task modulation effects. These two studies focused on different sets of brain regions and neither examined specifically the tool-selective regions systematically. Whether the tool-selective regions represent tool-use actions or the shapes of tools or both remains inconclusive. In another fMRI study (Fabbri et al., 2016), brain data were collected when participants performed different tasks (i.e., passive viewing, precision grip with two or five digits, or coarse grip with 5 digits) on arbitrary geometric objects (e.g., cube, sphere) with different shape, size or elongation. They found that elongation is particularly relevant for object-directed grasping and together with grasping properties is represented in the lateral occipital complex and middle temporal region close to the hand-tool selective area (Bracci et al., 2012) as well as in more dorsal parietal regions. However, tools are different from arbitrary geometric objects that they are associated with particular tool-use actions, which are not always transparent from shape, to achieve specific functional roles.

In the present study, we selected four daily tools (paintbrush, corkscrew, screwdriver, razor), where shape (I vs. T shape) and manners of manipulation (translation vs. rotation) properties were orthogonally related, to tease apart these two dimensions. We also collected behavioral ratings tapping on different aspects of actions to further examine the effects of potential finer action components. We collected fMRI data when participants viewed blocks of pictures of these four items. Information analysis (Peelen and Caramazza, 2012) and representational similarity analysis (RSA, Kriegeskorte et al., 2008) on the regional neural activation patterns were used to examine whether object shapes and action were represented in the tool-related network.

2. Materials and methods

2.1. Participants

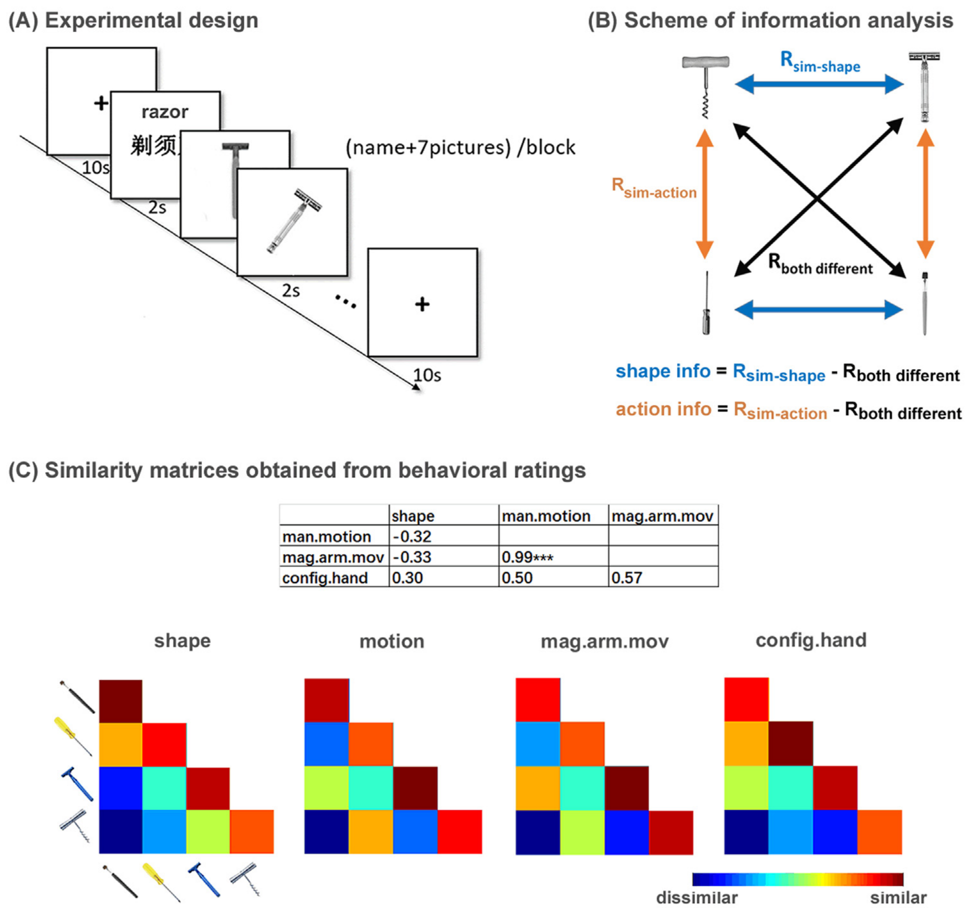
Twenty-two healthy college students participated in the task fMRI experiment. One participant had excessive head motion (>3 mm maximum translation or 2° rotation) in the main experiment but not in the tool-localizer experiment. Thus, 21 participants (14 females; age: mean $\pm$ SD $= 22 \pm 2$ years, age range: 19–26 years) with acceptable head motion were included in the analysis of the main experiment. All participants were right-handed (confirmed using Edinburgh handedness inventory (Oldfield, 1971)), had normal or corrected-to-normal vision and had no history of neurological or psychiatric disorders. The study was approved by the Institutional Review Board of the National Key Laboratory of Cognitive Neuroscience and Learning in Beijing Normal University. All participants gave written informed consent and received monetary compensation for their participation.

2.2. Experimental design and stimuli

All participants took part in a tool localizer experiment and an object verification fMRI experiment as well as a high-resolution T1 anatomical scan. The main experiment (object verification, Fig. 1A) was always followed by the tool localizer. In both experiments, picture stimuli were grayscale photographs (400 × 400 pixels, visual angle 10.55 × 10.55°). Participants viewed visual stimuli through a mirror attached to the head coil adjusted to allow foveal viewing of a back-projected monitor.

For the main experiment, four objects (i.e., paintbrush, razor, screwdriver, corkscrew) were selected to achieve a 2 × 2 orthogonal design (Fig. 1B) to dissociate shape (*T-shape* or *elongated*) from manipulation action (*rotation* or *translation*). Each object (e.g., paintbrush) has one counterpart which is similar in shape but different in manipulation (e.g., screwdriver), one similar in manipulation but different in shape (e.g., razor) and one different in both dimensions (e.g., corkscrew). Each object has 7 exemplars.

Given the focus of teasing apart shape and manipulation manner, the effects of finer tool-use action components were considered in a post-hoc fashion by collecting the ratings of these four experimental stimuli for further RSA analyses. Shape and potential action components (manner of motion, configuration of hand, magnitude of arm movement, inspired by Watson and Buxbaum (2014)) of the 4 objects were rated by an independent group of healthy college students (N = 20) using the multiple object arrangement method (Kriegeskorte and Mur, 2012). All 7 exemplars of each object were rated by each participant. Participants were told that the spatial distance between two



	shape	man.motion	mag.arm.mov
man.motion	-0.32		
mag.arm.mov	-0.33	0.99***	
config.hand	0.30	0.50	0.57

Fig. 1. (A) Design of the fMRI experiment; (B) Scheme of information analysis and (C) Similarity matrices of shape and different action components obtained from behavioral ratings by an independent participant group (N = 20) and the matrix of correlations between shape and action components. The color bar indicates the degree of similarity. Asterisks indicate significant correlation.

stimuli pictures indicated the similarity between them. For shape similarity judgment, participants were asked to arrange the stimuli pictures according to the perceived overall shape similarity of the objects, with examples denoting similar (orange - ball) and dissimilar (wolf - snake) pairs given as references. For manner of motion, participants were asked to arrange the pictures based on the similarity of the moving trajectories when using different objects, and the similar and dissimilar example pairs given were “key - light bulb” and “saw - key”, respectively; For magnitude of arm movement, participants were asked to arrange the pictures according to how similar amount the arm moved when using the objects, and the similar and dissimilar example pairs given were “ax-saw” and “ax-pen”;For configuration of hand, participants were asked to arrange the pictures based on the similarity of the hand posture, along with the similar example pair of “ax - shovel” and dissimilar example pair “ax - pen” given as references. The arrangements terminated when available time (i.e., 1 h) was up or the dissimilarity-evidence criterion (i.e., 0.5) was reached (Kriegeskorte and Mur, 2012). On average, it took about 30–40 min for each rating to stop for our participants. For each participant, a mean similarity score was obtained for each object pair by averaging similarity scores across all corresponding pairs of exemplars.

During the main fMRI experiment (Fig. 1A), participants viewed blocks of the four objects, with each block started with one object name and followed by 7 pictures of object exemplars. Participants were asked to judge whether all exemplars in the block was consistent with the object name by pressing corresponding buttons (all consistent, right index finger; otherwise, right middle finger). Participants were instructed to respond right after the disappearance of the last picture of each block as correctly and quickly as possible. Inconsistent blocks were assigned to one regressor of no interest (the “oddball” condition) when building general linear model (GLM) and were not included into subsequent analyses. Thus, all object conditions were supposed to be associated with identical button-press responses (i.e., right index finger press), ruling out the potential confounding of different motor responses.

Six runs were scanned for each participant. Each run lasted for 270 s, began and ended with a 10 s fixation period, during which a fixation cross was presented at the center of the screen. Each run was consisted of 10 task blocks (16 s each) separated by 10 s fixation periods. The 10 task blocks included two blocks per object and two oddball blocks within which inconsistent exemplars were presented. Each visual stimuli (i.e., object names and pictures) was presented for 2 s. The object exemplars presented in each block varied in four orientations (i.e., horizontal, vertical, 45°, 135°) to avoid visual adaptation. The orientation of object exemplars was balanced across different blocks. The block order was counterbalanced across runs.

A single-run tool localizer experiment was conducted to localize tool-selective regions. Participants viewed blocks of pictures of tools and large manmade objects and pressed a button with their right index finger as soon as possible when they detected a picture appeared twice in a row. Thirty pictures of different items were selected for each category for stimuli. The whole run lasted for 426 s in total, was consisted of 16 blocks, with 8 blocks per category. Fixation cross periods (10 s) were presented at the beginning and at the end of the whole run, as well as between blocks. Each block was consisted of 16 pictures (200 ms presentation, 800 ms fixation). The order of pictures was randomized across blocks and the presentation order of blocks was counterbalanced between categories. There were 0–2 catch trials per block. The number of button presses was matched between the two categories (8 times per category in total).

2.3. Image acquisition and preprocessing

All functional and structural MRI data were collected on a 3 T Siemens Trio Tim Scanner at the Beijing Normal University MRI center. For structural MRI, high-resolution anatomical three-dimensional magnetization-prepared rapid gradient echo (3D-MPRAGE) images were collected in the sagittal plane: 144 slices, repetition time (TR) = 2530 ms, echo time (TE) = 3.39 ms, Flip Angle (FA) = 7°, Matrix Size = 256×256, Voxel Size = $1.33 \times 1 \times 1.33\ mm^3$. BOLD fMRI data was collected using an echo-planar imaging (EPI) sequence that covered the whole cerebral cortex and the cerebellum: 33 axial slices, TR = 2000 ms, TE = 30 ms, FA = 90°, matrix size = 64×64, voxel size = $3 \times 3 \times 3.5\ mm^3$ with gap of 0.7 mm).

Data were preprocessed using Statistical Parametric Mapping software (SPM12; http://www.fil.ion.ucl.ac.uk/spm/software/spm12/). Preprocessing procedure included slice timing, head motion correction, low-frequency drifts removal with a temporal high-pass filter (cut-off: 0.008 Hz), and normalization into the Montreal Neurological Institute (MNI) space using unified segmentation. The functional images were resampled to 3 mm isotropic voxels and the data of the tool localizer experiment were further spatially smoothed using a 6 mm FWHM Gaussian kernel.

2.4. Data analysis

Functional data were analyzed using the general linear model (GLM) in SPM12. For the main experiment, the GLM included the 4 predictors corresponding to the 4 objects respectively, one predictor of no interest corresponding to the oddball condition (i.e., the two inconsistent blocks), along with 6 regressors of no interest corresponding to the 6 head motion parameters in each run. For the tool-localizer experiment, the GLM included 2 predictors corresponding to the tool and large manmade object categories respectively, along with 6 head motion parameters as covariates of no interest. Predictors were convolved with a canonical hemodynamic response function (HRF). For both experiments, participants with head motion > 2 mm or 2° in any direction were excluded from further analysis. Data analysis was performed within a gray matter mask (36272 voxels, 979,344 mm^3) which was defined as voxels with a probability higher than 0.4 in the SPM gray matter template and fallen into the cerebral regions (1# − 90#) in the Automated Anatomical Labelling (AAL) template (Tzourio-Mazoyer et al., 2002).

2.4.1. Definition of tool-selective regions of interest (ROI)

Tool-selective ROIs were defined as regions showing significantly stronger activation to tools relative to large manmade objects. Specifically, the contrast between tools and large manmade objects was measured for each voxel in each participant. A random-effects analysis was then conducted on the contrast maps of all participants to identify regions showing significant tool selectivity on a group level (FWE corrected $p < 0.05$ at cluster level, voxel $p < 0.001$, cluster size > 40).

In consideration that individual-based ROI analysis may be more sensitive, we also defined tool-selective ROIs in each individual participant for subsequent analysis. Specifically, the tool versus large manmade object contrast map in each individual was first thresholded at uncorrected $p < 0.05$. These thresholded individual contrast maps were then binarized and overlaid on top of one another. The value of each voxel in the overlaid map thus indicated the number of participants who showed stronger activation for tools versus large manmade objects at uncorrected $p < 0.05$ level. The voxels with value below 5 were excluded from the overlaid map and the resulting map was then transformed to a binary mask. At last, the intersection between each individual's tool vs. large object contrast map (uncorrected $p < 0.05$) and the binary mask was obtained and significant isolated clusters with cluster size > 50 voxels were identified for each individual participant as tool-selective ROIs.

2.4.2. ROI analyses

To investigate whether the tool-selective ROIs distinguish shapes or manipulation of objects, information analyses were conducted in each tool-selective ROI. In each ROI, multi-voxel activation pattern (t values) for each object was first extracted for each participant. For each voxel in each participant, the mean t value across the 4 objects was subtracted from each individual t value of each object (demeaning). The demeaning method was used to control for potential cross-voxel variability shared across different conditions (Sayres and Grill-Spector, 2008; Op de Beeck, 2010) which may drive high correlations between different conditions and thus mask the effect unique to each condition. In consideration that demeaning may affect the pattern and the interpretation of the results (Garrido et al., 2013), we also conducted analyses on raw data without demeaning. Pearson correlations were then calculated for all object pairs. As presented in Fig. 1B, the shape information was computed as the difference between the average of correlations between two objects similar in shape but different in action (i.e., screwdriver-paintbrush; corkscrew-razor) and the average of correlations between two object different in both dimensions (i.e., screwdriver-razor; corkscrew-paintbrush). The action information was computed as the difference between the average of correlations between two objects similar in shape but different in action (i.e., screwdriver-paintbrush; corkscrew-razor) and the average of correlations between two object different in both dimensions (i.e., screwdriver-razor; corkscrew-paintbrush). All correlations were Fisher transformed before information computation. Information values were tested against zero using one-sample *t*-test (one-tailed) with participants as random factor (N = 21). Note that for individual-based ROI analyses, the number of participants may vary across different ROIs since not all ROIs could be identified in all participants.

In addition to the focus of teasing apart shape and manipulation action, we also conducted RSA in a post-hoc manner to disentangle finer action components (i.e., configuration of hand, magnitude of arm movement, manners of motion). RSA using the distance judged by the independent rating group was also conducted on each ROI. Noteworthy that to achieve our primary goal of strongly disentangling shape and action, we could only find 4 particular tools, thus the RSA was restricted by the limited number of stimuli and the dissociation between different action components could not be simultaneously optimized. We correlated the extracted and demeaned (see above) multi-voxel activation patterns of the 4 objects, resulting in a 4×4 neural RSM per ROI and per participant. To investigate the independent representations of shape and different aspects of object-directed actions, partial correlations were computed between neural RSM and behavioral RSMs for shape and different aspects of actions, respectively, with all other remaining behavioral RSMs as controlled variables. Raw correlations without partialing were also computed and presented. Note that only values in the lower triangle (diagonal excluded) were used for correlation computation. The resulting correlation values were Fisher transformed and then entered into one-sample *t*-tests (one-tailed), with participants as random factor (N = 21).

Bonferroni correction was applied across the dimensions tested per ROI to avoid false-positives due to multiple comparison for both the information-based analyses (number of corrections = 2) and RSAs (number of corrections = 3).

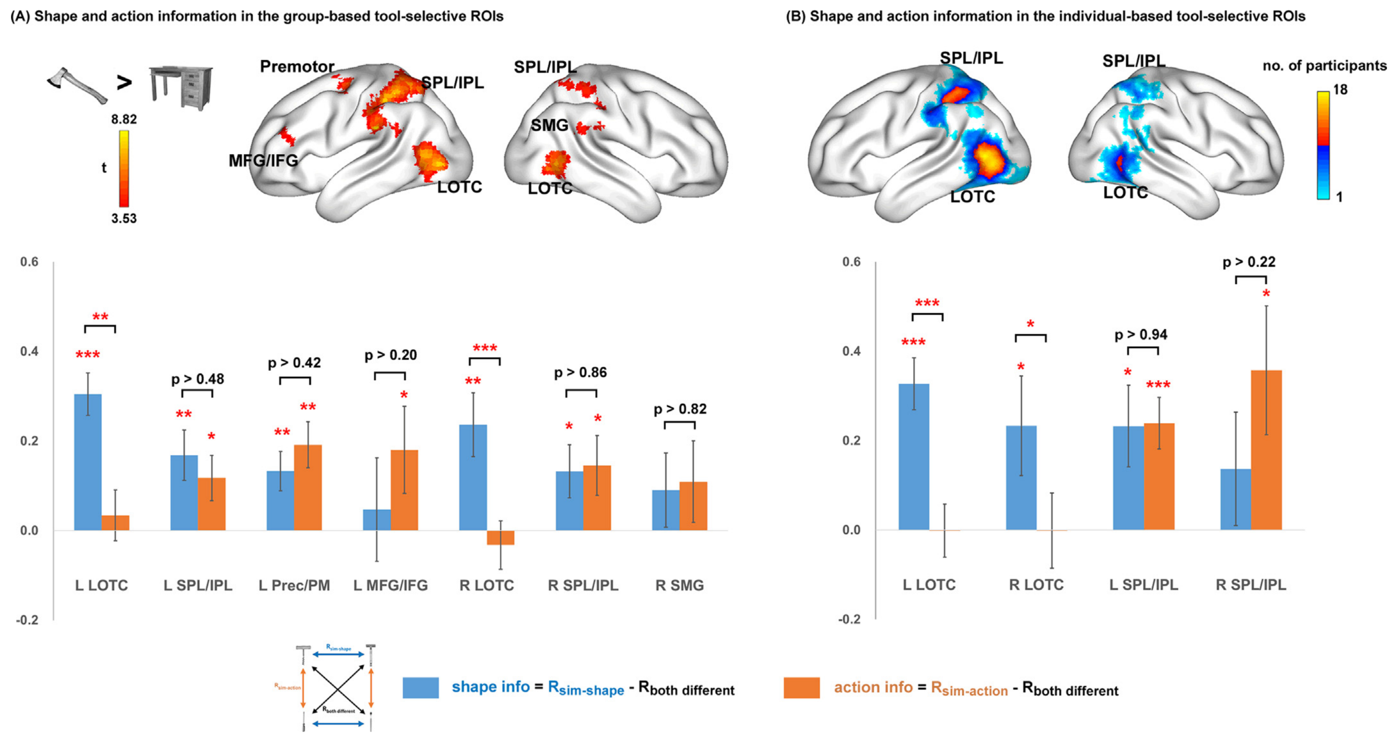


Fig. 2. Shape and action information in tool-selective ROIs. Information was computed as the difference between the mean correlation of object pairs similar in one dimension but different in the other and the mean correlation of object pairs different in both dimensions. (A) group-based ROI results. Top panel: tool-selective ROIs defined by the contrast of tools vs. large manmade objects at group level. Color bar indicates the t value of the contrast; Bottom panel: The shape (blue) and action (orange) information in each ROI. (B) individually-defined tool-selective ROIs (top panel) and ROI-based information results (bottom panel). Color bar in (B) indicates the number of participants in which tool-selective ROIs could be defined. Error bars in the bar plots indicate standard error. Asterisks indicate the significance level before multiple-comparison correction. *** , $p < 0.001$; **, $p < 0.01$, *, $p < 0.05$.

2.4.3. Whole–brain analyses

Whole-brain information searchlight analyses were conducted to find additional regions carrying significant shape or action information. Shape and action information were computed similarly as above for each search sphere (10 mm radius) centered on each voxel in the whole brain. The information values were then assigned to the center voxel and corresponding information maps were thus generated for each participant. A random-effects group analysis was performed on the spatially smoothed (FWHM = 6) information maps using the permutation-based statistical nonparametric mapping (SnPM; http://go.warwick.ac.uk/tenichols/snpm) to test for significant shape or action information. The significance threshold was defined as cluster-level corrected FWE $p < 0.05$ (voxel $p < 0.01$, variance smoothing = 0, permutation = 5000) for all analyses.

RSA searchlight analyses were also conducted to identify regions carrying representations of object shapes and different components of object-directed actions in the whole brain. For each search sphere (10 mm radius), the multi-voxel activation patterns were extracted for the four objects and correlated with each other to obtain a neural RSM. Correlations were computed between neural RSM and behavioral RSMs and the resulting r values then assigned to the center voxel, resulting corresponding r maps for each participant. The r maps were then Fisher-transformed and spatially smoothed (FWHM = 6) and entered to random-effects group analyses using SnPM. Similar threshold was used as in the information searchlight analyses.

All results in this paper are shown in the MNI space and projected onto the MNI brain surface using the BrainNet viewer (http://www.nitrc.org/projects/bnv/) (Xia et al., 2013).

3. Results

3.1. Behavioral results

In the main experiment, participants viewed blocks of pictures of corkscrew, paintbrush, razor and screwdriver and were asked to judge whether all pictures in each block were consistent with the cue word presented at the beginning of the block by pressing buttons. No significant difference was observed between the four object conditions on either response times (mean ± SE: paintbrush = 815 ± 123 ms, screwdriver = 736 ± 62 ms, corkscrew = 736 ± 61 ms, razor = 729 ± 75 ms; $F_{(3,87)} = 0.456$, $p = 0.716$) or accuracies (mean ± SE: paintbrush = 98.1% ± 13.6%, screwdriver = 98.0% ± 13.6%, corkscrew = 93.9% ± 23.9%, razor = 97.7% ± 14.9%; $F_{(3,87)} = 0.718$, $p = 0.544$).

When looking at behavioral ratings of finer components of object-directed actions (see Method), the manner of motion and the magnitude of arm movement was highly correlated with each other ($r = 0.99$, $p < 0.001$), and was not correlated with object shapes ($rs > -0.33$, $ps > 0.5$). The perfect correlation maybe because of the specific items we chose, which were rare cases where shape and manner of manipulation were strongly dissociated. The correlations between configuration of hand and object shapes as well as the other two action similarity measures were moderate ($rs = 0.30, 0.50, 0.57$, $ps > 0.2$). We thus combined the manners of motion and magnitude of arm movement to be the "kinematic" aspect of the object-directed actions (in contrast with hand configuration which corresponds to the more static, morphological aspects) by averaging these two measures for subsequent RSA.

Table 1
Group-defined tool-selective ROIs ($p < 0.05$, FWE corrected).

Area	Coordinates x	y	z	Peak t value (df = 21)	No. of voxels	Brodmann Regions
left SPL/IPL	− 27	− 48	54	8.82	738	1/2/3/4/5/7/22/40
left LOTC	− 51	− 66	6	8.00	319	18/19/21/22/37/39
left Prec/PM	− 24	− 9	57	6.49	124	6
left MFG/IFG	− 45	36	18	5.32	40	10/46
right LOTC	54	− 66	0	8.07	180	19/21/37/39
right SMG	60	− 33	27	5.61	73	40
right SPL/IPL	27	− 42	45	4.98	190	1/2/3/7

3.2. Shape and action representations in tool-selective ROIs

The whole-brain random-effects group analysis of the contrast of tool > large manmade objects (voxel $p < 0.001$, cluster size ≥ 40, FWE corrected $p < 0.05$ at cluster level) yielded the classical tool network: the bilateral LOTC encompassing the middle temporal gyrus and inferior and middle occipital gyrus, the bilateral superior/inferior parietal lobe (SPL/IPL) including the left supramarginal gyrus (SMG), the right SMG, the left precentral/premotor cortex (Prec/PM) and the left middle and inferior frontal gyrus (MFG/IFG) (Fig. 2A & Table 1).

To test for the object shape and action representations in these tool-selective ROIs, we first computed shape and action information for each ROI by subtracting the average of correlations between activation patterns to tools different in both dimensions from the average of correlations between activation patterns to tools similar in one dimension but different in the other (see Fig. 1 and Method). As presented in Fig. 2A and Table 2, one-tailed one-sample *t*-tests identified significant *shape* information in the bilateral LOTC, the bilateral SPL/IPL and the left Prec/PM cortex ($t_{(20)} > 2.24$. Bonferroni corrected $p < 0.05$). Significant *action* information was observed in the left Prec/PM cortex and bilateral SPL/IPL ($t_{(20)} > 2.17$, Bonferroni corrected $p < 0.05$) and in the left MFG/IFG at an uncorrected level ($t_{(20)} = 1.85$, uncorrected $p = 0.039$). No significant effect of either dimension was observed in the right SMG ($t_{(20)} < 1.20$, uncorrected $p > 0.122$, see Table 2 for detailed information). Directly comparing the magnitude of the two types of information using two-tailed paired *t*-tests, we found that shape information was significantly richer than action information in the bilateral LOTC (left: $t_{(20)} = 3.62$, $p < 0.002$; right: $t_{(20)} = 4.45$, $p < 0.001$). No significant difference between shape and action information was observed in other ROIs (ps > 0.13, Table 2). The patterns of results based on data without demeaning were largely similar (Supplementary Table 1).

We also conducted analyses in ROIs defined at individual subject level (see Method). As shown in Fig. 2B and Supplementary Table 2, we computed shape and action information in the individually defined ROIs which could be identified in at least 11 participants (> 50% participants), which were the bilateral LOTC and SPL/IPL ROIs. Similar as the results of the group-based ROI information analyses, the bilateral LOTC showed significant shape information (left: 0.33 ± 0.06, $t_{(19)} = 5.66$, $p < 0.001$; right: 0.23 ± 0.11, $t_{(12)} = 2.10$, $p < 0.029$) but insignificant action information (left: −0.002 ± 0.06, $t_{(19)} = 0.03$, $p = 0.510$; right: − 0.001 ± 0.08, $t_{(12)} = 0.01$, $p = 0.507$). The differences between shape and action information were significant in the bilateral individual-based LOTC ROIs as well (shape vs. action, left: $t_{(19)} = 4.10$, $p < 0.001$; right: $t_{(12)} = 2.38$, $p < 0.035$). The left SPL/IPL also exhibited similar pattern as in the results of group-based ROI analyses, containing both shape (0.23 ± 0.09, $t_{(15)} = 2.55$, $p < 0.011$) and action (0.24 ± 0.06, $t_{(15)} = 4.14$, $p < 0.001$) information in an indistinguishable manner (shape vs. action, $t_{(15)} = 0.07$, $p = 0.947$). While for the right SPL/IPL, the action information was still significant (0.36 ± 0.14, $t_{(10)} = 2.48$, $p < 0.016$) but the shape information become insignificant (0.14 ± 0.13, $t_{(10)} = 1.08$, $p = 0.152$). No significant difference was observed between shape and action information in the right IPL (shape vs. action, $t_{(10)} = -1.28$, $p = 0.230$). Frontal regions were not investigated due to low ROI identification rate across individual participants (< 7 participants). The patterns of results based on data without demeaning were largely similar (Supplementary Table 2).

We further carried out RSAs to test the effects of object shapes against potential finer action components (action kinematics and hand configurations) in the tool network using subjective measures. As shown in Table 3 and Fig. 3A, the neural RSMs of the bilateral LOTC and the left SPL/IPL ROIs were significantly correlated with the rating-derived object shape RSM ($t_{(20)} > 2.60$, Bonferroni corrected $p < 0.05$). After controlling for the effect of action kinematics and configuration of hand (Fig. 3B), the bilateral LOTC still showed significant shape representation ($t_{(20)} > 2.30$, Bonferroni corrected $p < 0.05$), while the shape effect in left SPL/IPL weakened ($t_{(20)} = 1.73$, uncorrected $p < 0.049$). Significant correlations with RSMs of action kinematics were identified in the left MFG/IFG and the left Prec/PM ROIs (Fig. 3A, $t_{(20)} > 2.72$, Bonferroni corrected $p < 0.05$). After controlling for the shape and configuration of hand (Fig. 3B), the action kinematics effect in the left MFG/IFG survived ($t_{(20)} = 2.49$, Bonferroni corrected $p < 0.05$) whereas those in the left Prec/PM ROI weakened ($t_{(20)} = 1.93$, uncorrected $p < 0.034$). The configuration of hand RSM correlated significantly with the neural RSMs of the bilateral LOTC, the left SPL/IPL and the left Prec/PM (Fig. 3A, $t_{(20)} > 2.82$, Bonferroni corrected $p < 0.05$). Weaker effects of hand configuration were also observed in the right SPL/IPL and SMG ROIs ($t_{(20)} > 1.88$, uncorrected $p < 0.05$). However, only the right LOTC remained to be correlated with the configuration of hand after controlling for object shape and action kinematics RSMs (Fig. 3B, $t_{(20)} = 2.32$, Bonferroni corrected $p < 0.05$). The patterns of results based on data without demeaning

Table 2
Shape and action information in group-defined tool-selective ROIs.

	Shape			Action			Shape vs. action	
	mean ± s.e.m	$t_{(20)}$	p	mean ± s.e.m	$t_{(20)}$	p	$t_{(20)}$	p
L LOTC	0.30 ± 0.05	6.45	< 0.001*	0.03 ± 0.06	0.60	0.278	4.19	< 0.001*
L SPL/IPL	0.17 ± 0.06	2.99	0.004*	0.12 ± 0.05	2.34	0.015*	0.71	0.484
L Prec/PM	0.13 ± 0.04	3.04	0.003*	0.19 ± 0.05	3.75	0.001*	− 0.81	0.426
L MFG/IFG	0.05 ± 0.12	0.41	0.343	0.18 ± 0.10	1.85	0.039	− 1.30	0.210
R LOTC	0.24 ± 0.07	3.32	0.002*	− 0.03 ± 0.05	− 0.59	0.719	3.85	< 0.001*
R SPL/IPL	0.13 ± 0.06	2.24	0.018*	0.15 ± 0.07	2.17	0.021*	− 0.17	0.863
R SMG	0.09 ± 0.08	1.09	0.144	0.11 ± 0.09	1.20	0.122	− 0.22	0.826

Note: P values shown in the table were uncorrected p values. Significant results after Bonferroni correction for multiple comparison (no. of corrections = 2) were denoted by asterisks.

Table 3
RSA results in group-defined tool-selective ROIs.

		r			Partial r (remove the other two variables)		
		mean ± s.e.m.	t	p	mean ± s.e.m.	t	p
shape	L LOTC	0.88 ± 0.12	7.41	< 0.001*	1.35 ± 0.20	6.77	< 0.001*
	L SPL/IPL	0.40 ± 0.15	2.60	0.008*	0.47 ± 0.27	1.73	0.049
	L Prec/PM	0.21 ± 0.16	1.32	0.100	0.35 ± 0.30	1.14	0.134
	L MFG/IFG	− 0.05 ± 0.19	− 0.27	0.604	0.05 ± 0.30	0.18	0.428
	R LOTC	0.78 ± 0.15	5.20	< 0.001*	0.73 ± 0.32	2.30	0.016*
	R SPL/IPL	0.25 ± 0.18	1.39	0.09	0.39 ± 0.24	1.62	0.060
	R SMG	0.25 ± 0.17	1.46	0.08	0.18 ± 0.30	0.61	0.275
action kinematics	L LOTC	− 0.13 ± 0.14	− 0.94	0.822	0.10 ± 0.32	0.30	0.385
	L SPL/IPL	0.23 ± 0.16	1.43	0.084	0.21 ± 0.24	0.89	0.193
	L Prec/PM	0.53 ± 0.16	3.41	0.001*	0.52 ± 0.27	1.93	0.034
	L MFG/IFG	0.49 ± 0.18	2.72	0.007*	0.63 ± 0.25	2.49	0.011*
	R LOTC	− 0.35 ± 0.13	− 2.61	0.992	− 0.36 ± 0.29	− 1.21	0.881
	R SPL/IPL	0.21 ± 0.19	1.07	0.149	0.34 ± 0.22	1.54	0.069
	R SMG	0.08 ± 0.17	0.51	0.309	− 0.02 ± 0.28	− 0.08	0.531
configuration of hand	L LOTC	0.35 ± 0.10	3.46	0.001*	0.08 ± 0.26	0.32	0.374
	L SPL/IPL	0.40 ± 0.11	3.65	0.001*	0.23 ± 0.21	1.10	0.142
	L Prec/PM	0.43 ± 0.09	4.74	< 0.001*	0.24 ± 0.24	0.99	0.167
	L MFG/IFG	0.10 ± 0.11	0.88	0.195	− 0.18 ± 0.21	− 0.84	0.795
	R LOTC	0.27 ± 0.09	2.82	0.005*	0.50 ± 0.21	2.32	0.016*
	R SPL/IPL	0.21 ± 0.11	1.88	0.038	− 0.02 ± 0.16	− 0.14	0.554
	R SMG	0.24 ± 0.12	1.96	0.032	0.22 ± 0.23	0.98	0.170

Note: p values shown in the table were uncorrected p values. Significant results after Bonferroni correction for multiple comparisons (no. of corrections = 3) were denoted by asterisks.

were largely similar (Supplementary Table 3).

3.3. Shape and action representations in the whole brain

Whole-brain information-based searchlight analyses were performed (Kriegeskorte et al., 2006) to uncover any additional brain

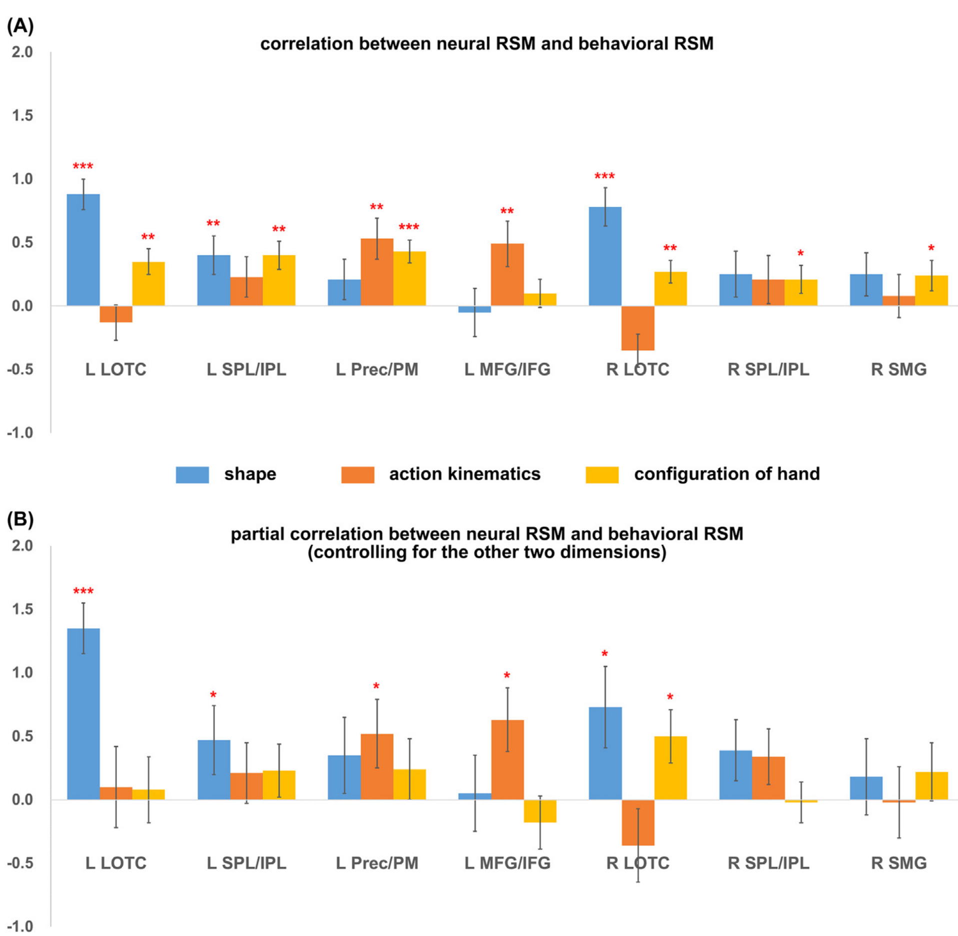


Fig. 3. RSA results based on the group-defined tool-selective ROIs. The bar plots show (A) correlations between neural RSMs and behaviorally derived RSMs on shape, motion/movement and configuration of hand; (B) partial correlations between neural RSMs and behaviorally derived shape, action kinematics and configuration of hand RSMs. For each behavioral RSM being tested, the two other models were controlled for to investigate the unique neural representation of the model being tested. Error bars in the bar plots indicate standard errors. Asterisks indicate the significance level before multiple comparison correction. ***, $p < 0.001$; **, $p < 0.01$, *, $p < 0.05$.

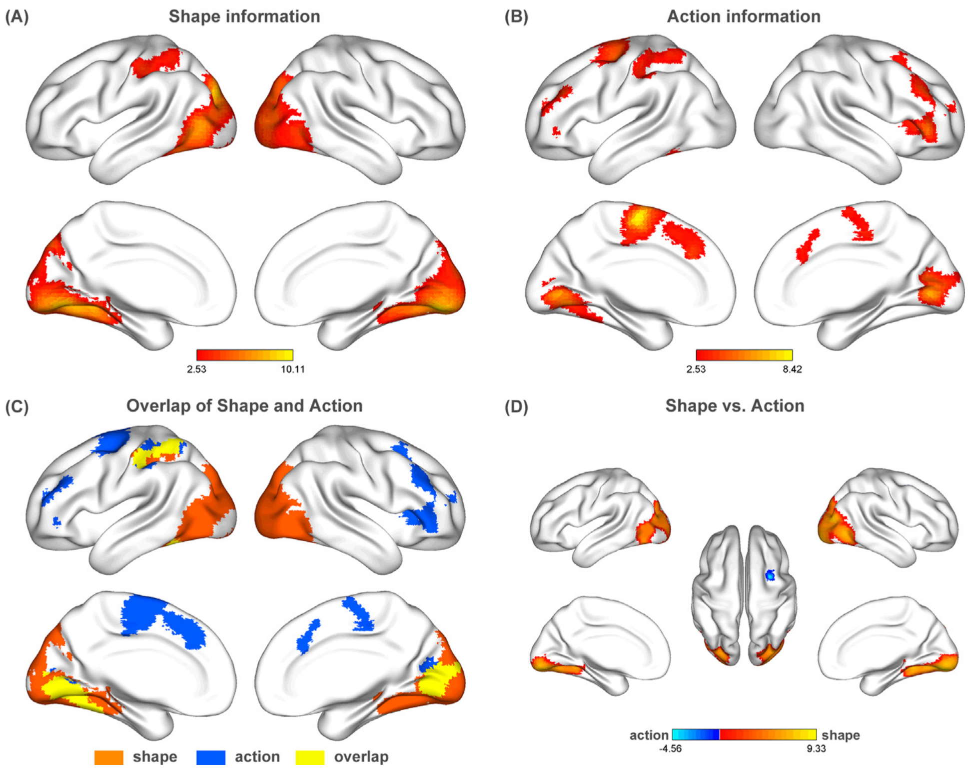


Fig. 4. Results of the whole-brain searchlight of (A) shape information and (B) action information; (C) the overlap (yellow) between shape (orange) and action (blue) information; and (D) the comparison between shape (warm-colored) and action (cold-colored) information. (A) and (B) were thresholded at FWE-corrected $p < 0.05$ at the cluster level, with the height threshold of $p < 0.01$; (D) was thresholded at uncorrected $p < 0.001$, cluster size > 10 voxels.

regions carry shape or action information. Significant shape information was observed in vast regions of the bilateral occipital cortex, inferior and middle temporal cortex and posterior inferior and superior parietal cortex (voxel $p < 0.01$, FWE corrected $p < 0.05$ at cluster level, Fig. 4A). Significant action information was observed in the bilateral supplementary motor area, precentral and premotor cortex, the right middle and inferior frontal cortex as well as the bilateral lingual gyrus (voxel $p < 0.01$, FWE corrected $p < 0.05$ at cluster level, Fig. 4B). As shown in Fig. 4C (yellow patches), significant information of both shape and action was observed in the left SPL/IPL (221 overlapping voxels) and the bilateral lingual gyrus (972 overlapping voxels). Comparison between the two types of information across the whole brain identified significantly stronger shape information in vast regions of bilateral occipitotemporal cortex (voxel $p < 0.001$, FWE corrected $p < 0.05$ at cluster level, warm colored clusters in Fig. 4D). Regions in the right middle frontal gyrus showed a trend of carrying more action information (uncorrected $p < 0.001$, cluster size > 10, cold colored clusters in Fig. 4D). Largely similar patterns were observed for results based on data without demeaning (Supplementary Fig. 1).

Whole-brain RSA searchlight analyses were also conducted to explore brain regions sensitive to finer aspects of tool-use actions. As shown in Fig. 5 (top left), the neural RSMs of vast regions of the bilateral occipital cortex, inferior and middle temporal cortex and a small portion of posterior SPL showed significant correlation with rating-derived shape RSM (voxel $p < 0.01$, FWE corrected $p < 0.05$ at cluster level). These regions remained to show shape effects after controlling for the effects of action kinematics and configuration of hand (Fig. 5, bottom left, voxel $p < 0.01$, FWE corrected $p < 0.05$ at cluster level). For action kinematics, significant correlations were identified in the bilateral MFG, IFG, supplementary motor area and precentral cortex (Fig. 5, top middle, voxel $p < 0.01$, FWE corrected $p < 0.05$ at cluster level). After controlling for object shape and configuration of hand, very similar regions remained significant and extended to the left anterior insula (Fig. 5, bottom middle, voxel $p < 0.01$, FWE corrected $p < 0.05$ at cluster level). Extensive regions of the left LOTC, bilateral posterior occipital cortex, bilateral calcarine and lingual gyrus, bilateral SMG, SPL and postcentral cortex and the bilateral precentral cortex showed significant correlation with RSM of configuration of hand (Fig. 5, top right, voxel $p < 0.01$, FWE corrected $p < 0.05$ at cluster level). After controlling for object shape and action kinematics, none survived the whole-brain multiple comparison corrections under this height threshold (Fig. 5, bottom right). Intriguingly, the right lingual gyrus and surrounding striate cortex showed significant unique effect of hand configuration under the threshold of voxel $p < 0.001$, cluster-level FWE $p < 0.05$. Largely similar patterns were observed for results based on data without demeaning (Supplementary Fig. 2) though the strength of effects slightly differed.

4. Discussion

In the current study, we tried to tease apart the shape and tool-use action using four tools for which these two dimensions were largely orthogonal. Information-based analyses revealed that within the tool network, the bilateral LOTC showed robust effects of shape but could not effectively distinguish between different object-directed actions; the left inferior frontal and precentral regions showed robust action effects; the left parietal region exhibited coding of both shape and action information. The RSA-based analyses, which allows for further tests of shape and finer action components based on post-hoc subjective ratings, confirmed the robust, unique representation of object shapes in the bilateral LOTC and action kinematic components in the left middle/inferior frontal and precentral regions. Beyond the tool-selective network, information-based and RSA-based whole-brain analyses consistently identified the lingual gyrus in coding of both shape and action information. Below we discuss our current findings in each of these regions.

4.1. The representation of object shapes in LOTC and its relation with object-directed actions

When disentangling shape from tool-use action information in the way that we do – i.e., selecting the rare cases where these two dimensions are fully dissociated – the tool-use action would have to be those can only be retrieved from memory instead of being computed

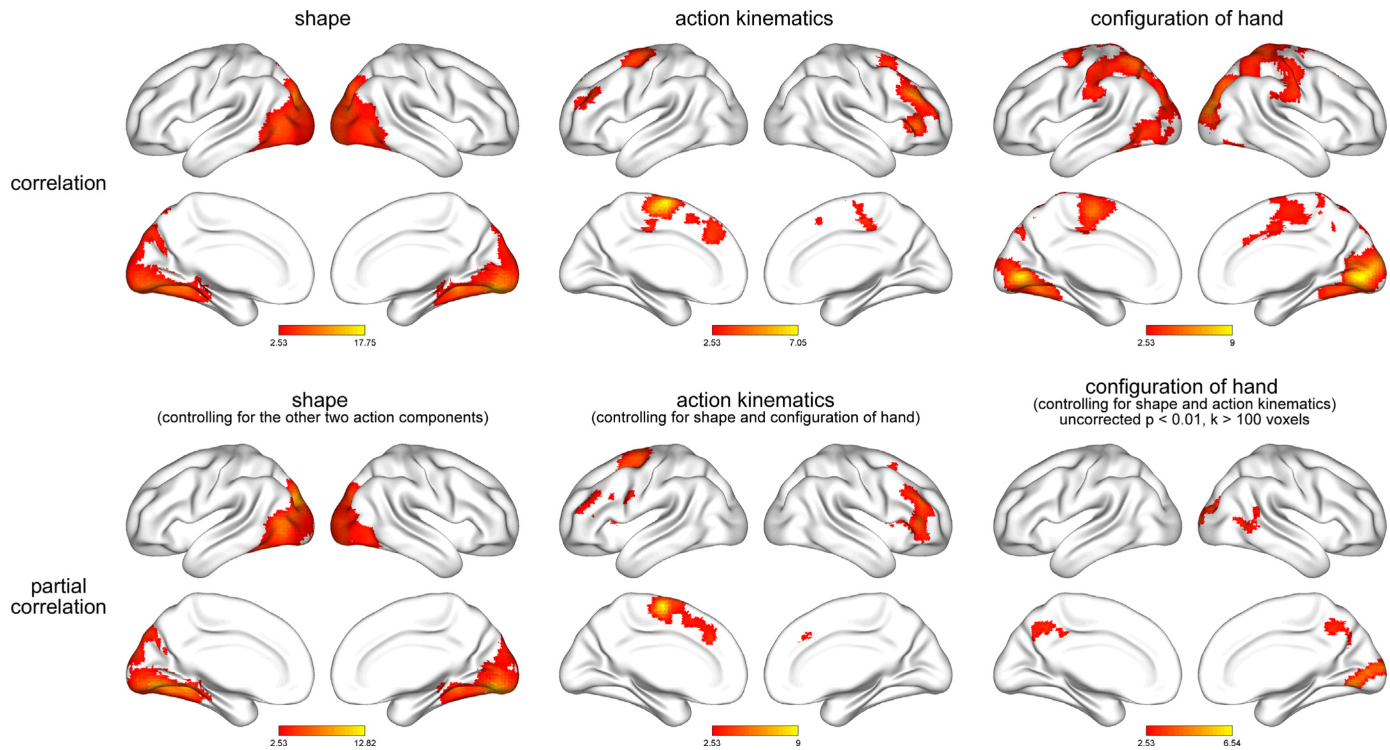


Fig. 5. Results of the whole-brain RSA searchlight. All maps were thresholded at FWE-corrected $p < 0.05$ at the cluster level, with the height threshold of $p < 0.01$, except that the bottom right map of the partial RSA result of the configuration of hand was thresholded at uncorrected $p < 0.01$, $k > 100$ voxels. Color bars denote t values.

from the object shape. In this case, we observed strong shape representation in the tool-selective LOTC and adjacent regions. This is consistent with the previous literature indicating LOTC's involvement in object shape representation (Peelen and Caramazza, 2012; Fabbri et al., 2016; Bracci et al., 2017; Chen et al., 2017a), and further indicate that the shape effects were independent from tool-use actions in LOTC. Objects are strongly represented in the LOTC according to their shapes (elongated objects together; T-shape objects together) regardless of the actions when people using them.

Although we found extensive regions of the visual cortex that could distinguish between T-shaped vs. I-shaped tools, tool-selective responses (contrasting tools with other objects) were observed in the LOTC but not in other (earlier) visual areas. While most visual areas are sensitive to (domain general) shape distinctions, it is likely that LOTC is more sensitive to certain ones that are associated with those related with tools. In addition, previous studies have found that in comparison to other ventral visual regions the LOTC was functionally connected with frontoparietal visuomotor areas frequently involved in action-related processing (Peelen et al., 2013; Hutchison et al., 2014; Hutchison and Gallivan, 2016; Chen et al., 2017a). The specific connectional profile may make this region an optimal relay station for transforming object shape information to dorsal motor-related regions for action planning (Mahon and Caramazza, 2011; Chen et al., 2017a). Interestingly, among the finer action components we tested, though we did not observe action kinematic representation in LOTC, we did observe significant correlation with hand configuration in this region before controlling for object shapes and action kinematics. It is possible that LOTC cares about shape and the shape-motor mapping (e.g., hand postures) of objects but not about other types of action knowledge that could not be computed from the object shapes. In line with this possibility, a series of studies have reported that LOTC encodes information about the hand-tool relationship (Bracci et al., 2012; Bracci and Peelen, 2013; Buxbaum et al., 2014) and grasping-related properties such as elongation of object shape, grasping axis or number of digits used during grasping (Monaco et al., 2014; Fabbri et al., 2016), indicating LOTC's involvement in representing object-hand interactions.

However, a large body of neuropsychological and neuroimaging studies have reported LOTC's involvement in action representation (Tranel et al., 2003; Kalénine et al., 2010; Watson et al., 2013; Tarhan et al., 2015; Wurm and Lingnau, 2015; Wurm et al., 2017; Bracci et al., 2017; Chen et al., 2017c; see Lingnau and Downing, 2015 for a review). Although in some of these studies the action representation might be correlated with object shapes (Chen et al., 2016, 2017b), most of these findings could not be simply accounted by the shape confound. However, these studies always used video or picture stimuli rich of explicit action information or used tasks requiring explicit retrieval of action information. Therefore, it is possible that the action effects in LOTC would only emerge when action information is apparent or is purposefully retrieved according to task demand. In our current study, we used tool picture stimuli which do not contain explicit action information and adopted a word-picture verification task which does not necessarily engage action retrieval. It is thus possible that experiments with an explicit action task and/or with stimuli directly conveying action information could better reveal the action representations in the LOTC (but see Bracci et al., 2017). Moreover, to achieve our primary goal of strongly disentangle shape and action we have a very limited stimuli space and could only found 4 particular tools, the dissociation between different action components could not be simultaneously optimized (e.g., the high correlation between manners of motion and magnitude of arm movement). Future studies using larger set of tools could be conducted to test the generalizability of our findings and better reveal how different action components related with shape and how they were represented in the tool network.

4.2. Shape and action representations in the parietal cortex

The inferior and superior parietal lobe have been considered as part of the dorsal visual system, which has classically been implicated in visuomotor control rather than object shape and identity representations (Goodale et al., 1992; Milner and Goodale, 2006; Freud et al., 2016). However, recent studies have found non-action-based object representations in the parietal regions (Konen and Kastner, 2008; Zachariou et al., 2014; Bracci and Op de Beeck, 2016; Jeong and Xu, 2016) which challenge the binary functional dissociation between ventral and dorsal visual pathways. In line with the recent findings, we observed significant shape representation in posterior and superior parietal regions. The shape representation in the posterior parietal region, though being weakened, remained to show a trend even after controlling for the effects of action components. Previous findings showed that posterior parietal object regions are sensitive to viewpoint changes (James et al., 2002; but see Konen and Kastner, 2008). It is thus possible that the shape representation in parietal cortex may be different from those in occipitotemporal cortex, with the latter more invariant and similar to the perceived object shapes whereas the former more dependent on the viewpoints and similar to the physical shapes. With a blocked design, our experiment could not distinguish between different shape representations. It would be interesting for future studies using item-wise experimental design to investigate the possible dissociable representations of object shapes and their relationship with object-directed actions in the ventral occipitotemporal cortex and the dorsal parietal cortex.

Combining results from both ROI-based and whole-brain information analyses, voxels in the posterior part of the superior parietal lobe showed significant coding of both shape and action information, which is consistent to a recent study showing that this region similarly coded object (i.e., elongation, shape) and grasp (i.e., number of digits) property (Fabbri et al., 2016). Together with previous findings (Buxbaum et al., 2005, 2014; Goldenberg, 2009; Kalénine et al., 2010), these results suggested a critical role of the parietal cortex in the representation of both object shape properties and a broad range of action properties (grasping, hand configurations and manners of motion). However, when looking at finer action components, the RSA analyses identified neither significant, unique representation of object shapes nor of specific action components (action kinematics and hand configuration) in the parietal lobe. Whether these null results indicate representation of information communal to both object shape and multiple action components in the parietal cortex, or they were merely due to the restriction of the current experimental design (too few datapoints for the RSA), needs further investigation.

In addition, it would be also interesting to investigate whether the shape or action representation in the parietal cortex was modulated by task demands. Previous studies gave conflicting results to this question (Bracci et al., 2017; Chen et al., 2017). Chen et al. (2017) reported that the action representation in parietal cortex was independent of tasks and stimuli types (i.e., pantomime to printed tool words; object picture identification); Bracci and colleagues (Bracci et al., 2017) showed that neural representation in parietal cortex was task-relevant (i.e., action/shape representation in action task, category representation in category task). Future researches investigating the task effects on the neural representation of parietal cortex may deepen our understanding of tool-related processing in this region.

4.3. The representation of tool-related actions in frontal cortex

Our findings about the coding of tool-related action components (action kinematic components) in precentral/premotor and inferior/middle frontal cortex is in line with the idea that the frontal cortex is a component of human mirror neuron system and plays critical role in action understanding (Rizzolatti and Craighero, 2004; Rizzolatti and Sinigaglia, 2010; Rizzolatti et al., 2014). Intriguingly, recent studies that reported unimodal and relatively concrete action representations in frontal cortex seem to challenge its involvement in representing stored action knowledge (Negri et al., 2007; Watson et al., 2013; Wurm and Lingnau, 2015; Chen et al., 2017b). Instead this area could be part of the "dorsal-dorsal" structure system specialized for online processing of actions based on the current object visual information (Buxbaum and Kalenine, 2010; Buxbaum, 2017), which was distinct from the learning-based manipulation knowledge about tool use. Thus, it is possible that the pattern we observed here was due to participants' automatic simulation of the tool-related actions, which is in line with the proposal that the activation of motor information in the "dorsal-dorsal structure system" may be outside of conscious awareness and require no particular intention or goals (Buxbaum and Kalenine, 2010). Whether there is a separate system that represents tool use action knowledge and whether frontal cortex plays a role in it need further investigations.

4.4. Unexpected findings: the coding of shape and action information in lingual gyrus

In addition to the frontoparietal and occipitotempral regions frequently involved in tool-related processing, information-based and RSA-based whole-brain analyses revealed representation of both shape and action information in lingual gyrus. The lingual gyrus contains the ventral part of V2 (Clarke and Miklossy, 1990), which was frequently involved in visual shape processing (e.g., Hegdé and Van Essen, 2000, 2004). It is thus not surprising to observe robust shape discrimination in this region. However, the coding of action information in the lingual gyrus was unexpected. We do not have a natural explantion for this piece of result and could only speculate that it might be driven by some unknown relationship between visual properties and action in our stimuli set.

5. Conclusion

By teasing apart tool shape and tool-use action, we observed a functional dissociation between occipitotemporal and frontal tool-selective regions in representing shape information and action, and a communal representation of both properties in the parietal cortex (in information analyses). These results clarify the nature of the representation contents in terms of these two dimensions within the tool network, and suggest the further examinations of finer level shape and action components being computed and connected in this network.

Acknowledgement

This work was supported by the National Key Basic Research Program of China (2014CB846100 to Y.B.), National Natural Science Foundation of China (31500882 to X.Y.W., 31671128, 31521063 to Y.B.), the Fundamental Research Funds for the Central Universities (2017XTCX04), the National Program for Special Support of Top-notch Young Professionals (Y.B.), the Interdiscipline Research Funds of Beijing Normal University (Y.B.).

Conflict of interest

The authors declare no competing financial interests.

Author contributions

Y.B. and X.W. designed research; T.Z. and J.S. performed research; T.Z. and X.W. analyzed data; X.W. and Y.B. wrote the paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2018.05.026.

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